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OFFSPRING SIZE AFFECTS THE POST-METAMORPHIC PERFORMANCE OF A COLONIAL MARINE INVERTEBRATE

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Abstract. The positive relationship between offspring size and offspring fitness is a fundamental assumption of life-history theory, but it has received relatively little attention in the marine environment. This is surprising given that substantial intraspecific variation in offspring size is common in marine organisms and there are clear links between larval experience and adult performance. The metamorphosis of most marine invertebrates does not represent a ''new beginning,'' and larval experiences can have effects that carry over to juvenile survival and growth. We show that larval size can have equally important carryover effects in a colonial marine invertebrate. In the bryozoan *Bugula neritina*, the size of the non-feeding larvae has a prolonged effect on colony performance after metamorphosis. Colonies that came from larger larvae survived better, grew faster, and reproduced sooner or produced more embryos than colonies that came from smaller larvae. These effects crossed generations, with colonies from larger larvae themselves producing larger larvae. These effects were found in two populations (in Australia and in the United States) in contrasting habitats.

Key words: *bryozoan;* Bugula neritina; *carryover effect; maternal effect; reproductive success.*

INTRODUCTION

A central tenet of life-history theory is the presence of a trade-off between the size and number of offspring that a female can produce for a given clutch (Stearns 1992). Producing many, small offspring may spread the risks of mortality, but with a shift to fewer, larger offspring, these benefits must be offset by higher individual fitness for larger offspring (Smith and Fretwell 1974), so a crucial component of this hypothesis is that larger offspring have greater fitness than smaller offspring (Sinvero 1990). Indeed, many studies show a relationship between offspring size and initial offspring fitness (Stearns 1992, Williams 1994, Bernardo 1996). However, this relationship is by no means universal, and smaller offspring can, in some cases, have relatively higher survivorship as juveniles (reviewed in Moran and Emlet [2001]).

Offspring size may not affect fitness as expected because in some cases no such link exists. For example, variation in environmental quality may alter the advantages of producing larger offspring, especially under benign conditions or periods of abundant food (Reznick and Yang 1993, Mousseau and Fox 1998). Alternatively, a link may be missed because key components of fitness cannot be measured or are examined at insufficient temporal or spatial scales. This might occur because the juveniles or adults are highly dispersive, time to maturity is very long, or reproduction occurs over an extended period. If an effect of offspring size only becomes apparent in later adult life, studies that focus on early stages may incorrectly conclude that offspring size has no effect.

While the link between offspring size and fitness is central to life-history theory, there are few tests of this relationship in marine organisms (Moran and Emlet 2001). In one of the notable exceptions, Moran and Emlet (2001) found strong effects of offspring size on juvenile and adult survival, growth, and time until maturity in the intertidal gastropod *Nucella ostrina*. The lack of studies on other marine species is surprising, given the wide variation in offspring size among and within marine invertebrate species, especially in light of the established link between larval condition and post-larval performance in many species (reviewed by Pechenik et al. [1998]).

Marine invertebrates exhibit a wide range of larval sizes within and among populations and between species. In a number of species, egg size varies with maternal body size, habitat quality, and maternal nutrition (e.g., George 1996, Jones et al. 1996, Bertram and Strathmann 1998, Marshall et al. 2000) . Variation in egg size, even within an individual brood, can lead to larvae of varying sizes (Marshall et al. 2002). The consequences of this variation remain largely unexplored.

Recently, it has been recognized that larval experiences of marine invertebrates, such as stress or prolonged swimming time, can have carryover effects on juvenile growth and survival (Pechenik et al. 1998), despite the massive tissue reorganization associated with metamorphosis. In non-feeding (lecithotrophic) larvae, these effects presumably occur because the en-

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ergetic reserves available for metamorphosis and early growth are depleted (Pechenik et al. 1998). For example, Wendt (1998) found that when larvae of the bryozoan *Bugula neritina* had their energetic reserves decreased by prolonged swimming, the subsequent colonies had relatively lower growth rates and fecundity in the field. Another, unexplored source of carryover effects may be larval size, as different-sized larvae will have different nutritional reserves.

Here, we test whether variation in larval size in one such species, the arborescent bryozoan *Bugula neritina*, affects a range of fitness-related post-larval traits. We collected adult colonies, obtained larvae from them, and allowed the larvae to settle in the laboratory. We then transplanted the metamorphosed juveniles to the field, where we measured subsequent growth and survival, adult reproduction, and size of offspring in the next generation. Because the effects of offspring size could vary in different environmental conditions, we repeated the experiments at two very different localities.

METHODS

Study species and sites

Bugula neritina adults are sessile, grow by asexual budding, and, when reproductive, they brood larvae in obvious brood structures (ovicells) and can easily be induced to release larvae. Larvae spend only a short time in the plankton, existing on internal energy reserves. *Bugula neritina* is a cosmopolitan species, although recent molecular evidence suggests the presence of two morphologically indistinguishable species in California (Davidson and Haygood 1999). Material from other areas around the world corresponds to one of these types (Davidson and Haygood 1999; J. Mackie, *personal communication*).

In Australia, experiments and collections of sexually mature colonies were done at Breakwater Pier in Williamstown, Victoria, during January–February 2000. The site has low wave energy, and water temperature for the experimental period was 18–21°C. A second set of collections and experiments was done in the United States, at the University of South Florida's St. Petersburg campus dock during July–August 2000. The site was less sheltered than Williamstown and thunderstorms were frequent. Surface water temperature was 28–29°C during the experiments.

General experimental methods

Colonies collected from Williamstown were maintained in a recirculating seawater system at 15°C for up to three days. Colonies collected from St. Petersburg were maintained at the University of South Florida in plastic aquaria at 28°C for up to two days. Colonies from both sites were held in the dark and received no supplemental food. Colonies were removed from the dark, placed in clean glass beakers with 500 mL of seawater, and exposed to bright light for ≈30 min. Release of larvae began within 15 min of illumination and continued for up to one hour. Approximately 20 min after spawning began, larvae were collected using a syringe and placed into clean 15-mL scintillation vials. They were then pipetted onto a microscope slide with a small drop of water in which they could swim. We briefly videotaped individual larvae using a video microscope under 40× magnification. From each video sequence, we selected a frame in which the larva was oriented with the ciliated groove facing directly upwards, digitized the image, and measured the larva (SigmaScan Version 3, SPSS, Chicago, Illinois, USA, was used in Australia; Image-Pro Plus Version. 4, Media Cybernetics, Silver Springs, Maryland, USA, was used in Florida). We measured the length of the ciliated groove and the widest point perpendicular to that groove to the nearest micron. The values were then multiplied to estimate larval cross-sectional area. Pilot studies showed that this measure was a good predictor of larval volume ($r^2 = 0.93$, $n = 30$).

Experiment 1: Relationship between colony size and larval size

To test the relationship between colony size and offspring size we collected 11 sexually mature colonies from Williamstown and six colonies from St. Petersburg. The colonies were induced to spawn and 10 larvae from each colony were measured to the nearest micron. After spawning, the colonies were gently dried with paper toweling and weighed to the nearest milligram.

Experiment 2: Effects of larval size

To investigate the effects of larval size on larval fitness we collected a new set of broodstock colonies. We repeated this experiment four times at St. Petersburg and three times at Williamstown. For each of the seven experimental runs, we used larvae spawned from a new group of 4–10 colonies. To avoid the potentially confounding effect of parental colony size, all colonies were of equal size (10 bifurcations per colony). Each colony was spawned in its own beaker, and care was taken to ensure that large and small larvae from each colony were used, so the larvae used for each run were genetically mixed, with a wide range of sizes. After measuring each larva, we placed it onto its own dark Perspex (Plexiglas) 50 × 30 mm settlement plate. The plates were roughened with sandpaper and kept in seawater for at least 24 h before exposing them to larvae. Individual larvae were pipetted with ~500 μL of seawater into a small polyethylene tube that sat on top of the Perspex plate. A watertight seal between the tube and the plate was maintained by applying a small amount of silicon grease to the base of the tube. About half of the larvae attached to the plate; any that attached on the polyethylene tube or the few that failed to attach within one hour of spawning were discarded. Larvae

that failed to attach did not differ in size to those that did attach (D. Marshall, *unpublished data*). We then removed the tube and returned the settlement plate to an aquarium for 24 h. The plates were then transported in insulated containers to the field. Settlement plates were bolted onto a large (70 cm × 70 cm) Perspex backing plate. The positions of the settlement plates on the backing plate were determined haphazardly. A separate backing plate was used for each experimental run. At Williamstown, the backing plate was hung face down to reduce the effects of light and sedimentation, at a depth of 2 m below the mean low water mark. At St. Petersburg, the pylons were too close together for the backing plates to be suspended face down, so they were suspended vertically with the middle of the backing plate ~2.5 m below the mean low water mark. Runs were started roughly five days apart. St. Petersburg runs used 22, 19, 13, and 10 larvae in each; Williamstown runs involved 22, 19, and 11 larvae.

For each run, the size and mortality of the colonies were recorded 7, 14, and 30 days after deployment into the field. Each time, we retrieved the backing plates and placed them in seawater-filled tubs. Measurement of the colonies took ~10 min, after which they were immediately returned to the water. The size of colonies was measured here following Keough and Chernoff (1987). As *Bugula neritina* grows, the colony bifurcates at regular intervals, and by counting the number of bifurcations on a line from colony base to tip, the number of zooids in each colony can be estimated. Fecundity was measured as the number of ovicells visible on the colony. Size and fecundity of colonies were also recorded at Williamstown 28, 35, and 42 days after deployment for two runs. Finally, at day 55, an experimental run from Williamstown was brought back to the laboratory where the colonies were maintained in dark, flow-through aquaria. The next day we exposed the colonies to light and collected all the larvae released from each colony. We fixed the larvae with a few drops of formalin and later measured them. Pilot studies indicated that fixation had no effect on larval size (D. Marshall, *unpublished data*).

Data analysis

We used analysis of covariance (ANCOVA) to examine the effect of parental colony size on mean larval size at the two sites. Two colonies were omitted to equalize the ranges of parental colony sizes (covariates) between both sites (Quinn and Keough 2002). To examine the effect of larval size on mortality, we used logistic ANCOVA for each site where larval size was the covariate and experimental run was a categorical variable. No interaction between run and larval size was detected so we then ran a reduced model with the size × run interaction term removed. For Williamstown, we examined survival 14 days after deployment in the field, as no further mortality occurred after this time. For St. Petersburg, we examined survival of four runs 14 days after deployment in the field. In addition, for the first three runs at St. Petersburg, we repeated the analysis on survival after 30 days in the field (Run 4 only ran for 14 days). To examine the effect of larval size on colony growth we used repeated-measures ANCOVA where experimental run was a random factor and larval size was a covariate. At St. Petersburg, there was no interaction between larval size and experimental run, so this term was omitted, and analysis using a reduced model was used. At Williamstown, each run had a very different duration (e.g., Run 1 = 8 wk, Run 3 = 4 wk), so we performed separate repeated- measures ANCOVA for each run for both colony size and colony reproduction (measured as number of ovicells per colony) where larval size was a covariate.

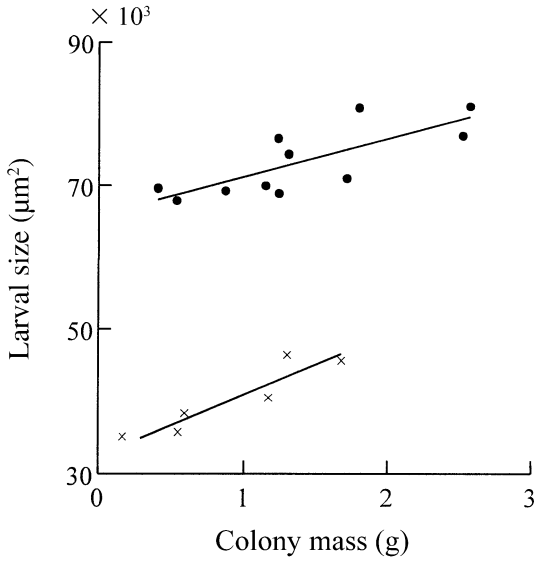

FIG. 1. Relationship between colony size (wet mass) and offspring size of *Bugula neritina* colonies from Williamstown, Australia (circles), and St. Petersburg, USA (crosses). Each point represents the mean of 10 larvae from a single colony. Note that the two largest Williamstown colonies were excluded from the ANCOVA.

RESULTS

The mean size of larvae increased with parent colony wet mass in *Bugula neritina* from St. Petersburg and Williamstown (ANCOVA, effect of colony size: $F_{1, 12} = 18.11$, $P = 0.001$; slopes not heterogeneous, $F_{1,11} = 0.51$, $P = 0.492$). Larvae from Williamstown were much larger than larvae from St. Petersburg (ANCOVA, effect of site: $F_{1,12} = 351.49$, $P < 0.0005$; Fig. 1).

Mortality was consistently much higher in St. Petersburg than at Williamstown (mean total mortality ± 1 SE: 77.4 ± 5.8% and 38.5 ± 6.8%, respectively), even though colonies in Williamstown were in the field for up to three weeks longer than the Florida colonies. At Williamstown, most mortality occurred in the first week after settlement and no mortality occurred after two weeks. In Florida, the daily mortality rate (cal-

TABLE 1. Logistic ANCOVA of the effects of larval size and experimental run on colony survival in the field at Williamstown (Victoria, Australia) and St. Petersburg (Florida, USA) 14 days and 30 days (Florida only) after settlement.

Site and parameter	Odds ratio	χ^2	*P*
Williamstown (14 days; 3 runs)			
Larval size	1.00	8.60	0.003
Run		5.91	0.052
Size × run		1.64	0.440
McFadden's ρ^2			0.291
Florida (14 days; 4 runs)			
Larval size	1.01	7.40	0.007
Run		4.04	0.257
Size × run		3.06	0.382
McFadden's ρ^2			0.167
Florida (30 days; 3 runs)			
Larval size	1.00	2.26	0.132
Run		1.39	0.500
Size × run		3.97	0.167
McFadden's ρ^2			0.063

Notes: The test of heterogeneity of slopes was made as an initial step, followed by fitting of a reduced model. Wald tests were used to assess the significance of particular effects, with degrees of freedom of 1 for size effects and number of runs − 1 for other effects.

culated as the percentage of individuals that died per day) was greatest in the first week after settlement (daily mortality ~6%), although mortality continued throughout the study period (daily mortality ~3.75%). Periods of high mortality in Florida appeared to be associated with storms.

At Williamstown, mortality was strongly size dependent, with colonies that originated as larger larvae having much higher survivorship than colonies that originated from smaller larvae in all three runs (Table 1). Larval size varied by a factor of >2, and across this range, survivorship ranged from 7% to 97% (calculated from logistic regression equation), with larval size and runs explaining a good proportion of variation in survivorship (see McFadden's ρ^2 value, Table 1). In Florida, colonies from larger larvae were more likely to survive than smaller colonies in the first 14 days after settlement but we could not detect an effect of colony size after 30 days in the three runs for which we had data (Table 1). There was a more than twofold range in larval cross-sectional areas, and survivorship after 14 days increased over this range from near zero to nearly 100%, although there was considerable noise in the relationship (Table 1).

Colony growth rates were generally higher in Florida than Williamstown. In Florida, larval size affected colony size but this relationship changed with time (Table 2). This interaction may have occurred because high mortality rates resulted in very few live individuals two weeks after transplanting plates into the field. At Williamstown, colony size at any time appeared to be much more strongly related to larval size than in Florida (Fig. 2). In each run there was a strong effect of larval size on colony size and we could detect no effect of time on this relationship (i.e., no interaction between larval size and time; Table 3).

In both runs at Williamstown where reproduction was assessed, the number of ovicells per colony increased with original larval size but in Run 1 this relationship changed with time (Table 3). In Run 1, reproduction began almost simultaneously among all colonies, with no relationship between larval size and onset of reproduction ($r = -0.328$, $n = 10$, $P = 0.353$; Fig. 2). In Run 1, eight weeks after settlement, the number of larvae released per colony also increased with original larval size ($r = 0.754$, $n = 9$, $P = 0.019$). In Run 2, colonies that came from larger larvae began reproducing sooner (comparison of larval size and onset of reproduction, $r = -0.678$, $n = 13$, $P = 0.011$; Fig. 2).

Colonies in Run 1 that originated from larger larvae released larger larvae themselves ($r = 0.758$, $n = 9$, $P = 0.018$; Fig. 2). Larvae derived from the largest original larvae were approximately twice the volume of those derived from small larvae.

DISCUSSION

At both Williamstown and St. Petersburg, larger *Bugula neritina* colonies produced larger larvae, and colonies from Williamstown produced larger larvae than colonies of equivalent size from St. Petersburg. The ultimate causes of variation in larval size are unclear. Larger colonies could be investing more energy per larva as they allocate less energy to growth. Alternatively, if larger colonies contain older or larger zooids than smaller colonies, the characteristics of the zooids themselves may account for the observed variation in larval size. Sakai and Harada (2001) suggest that larger parents may provision their offspring more efficiently and can therefore produce larger offspring at a lower energetic cost than smaller parents.

Larval size had broad and persistent effects well beyond metamorphosis. The effects of larval size on subsequent colony performance observed here are independent of parental colony size as we used similar sized

TABLE 2. Analysis of the effect of larval size on *Bugula neritina* colony growth in the field for three experimental runs at St. Petersburg, Florida, USA.

Source	df	MS	*F*	*P*
Between subject				
Larval size	1	4.96	11.94	**0.013**
Experimental run	2	1.35	2.97	0.116
$MS_{Residual}$	7	0.45		
Within subjects				
Time	2	0.69	0.43	0.675
Time × larval size	2	2.78	11.15	**0.001**
Time × run	4	1.58	6.36	**0.004**
$MS_{Residual}$	14	0.25		

Notes: Colonies for each run were in the field for 30 days. *P* values <0.05 are shown in bold type.

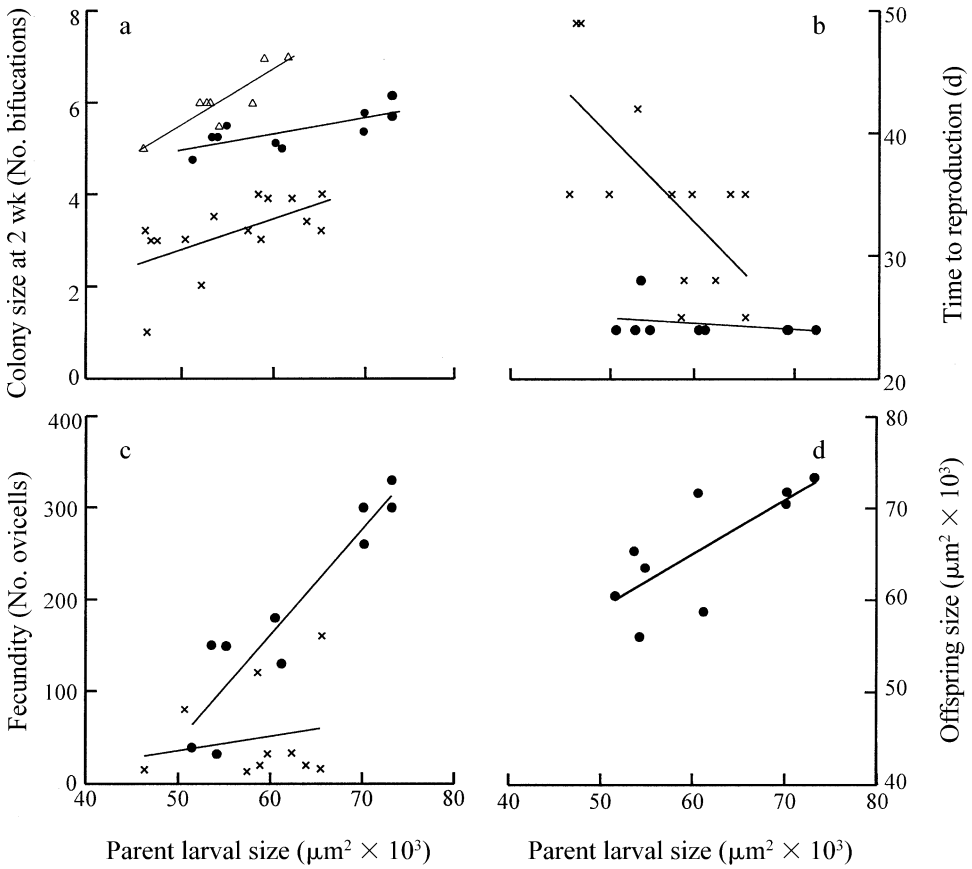

FIG. 2. Relationships between original parent larval size and (a) colony growth, (b) time to reproduce, (c) fecundity, and (d) offspring larval size of *Bugula neritina* at Williamstown, Australia. Runs are denoted with different symbols: Run 1 (circles), Run 2 (crosses), and Run 3 (triangles). In panel (d), each point represents the mean size of 20 larvae from a single colony. Note that the scale numbers for parent larval size and for offspring size indicate thousands of square micrometers.

parent colonies within each experimental run. Initial mortality of *Bugula neritina* colonies was strongly related to larval size at both sites, and this pattern persisted for at least weeks at Williamstown. The mortality rates observed here are far below those reported for *B. neritina* and other sessile marine invertebrates although, as in other studies, the majority of mortality occurs early after settlement (reviewed in Keough

TABLE 3. Analysis of the effect of larval size on *Bugula neritina* colony growth and reproduction in the field at Williamstown, Australia.

	Growth						Reproduction			
	Run 1		Run 2		Run 3		Run 1		Run 2	
Source	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Between subjects										
Larval size	6.84	**0.031**	7.55	**0.017**	11.13	**0.029**	22.79	**0.001**	5.45	**0.037**
$MS_{Residual}$	2.2		2.8		1.1		8409		6199	
Within subjects										
Time	2.33	**0.047**	4.00	**0.007**	0.10	0.910	3.72	**0.047**	1.06	0.364
Time × larval size	1.74	0.133	0.46	0.763	0.24	0.791	8.61	**0.003**	2.25	0.128
$MS_{Residual}$	0.28		0.22		1.24		2805		2892	

Notes: The numbers of time periods where growth was assessed for Runs 1, 2, and 3 were 7, 5, and 3, respectively. The number of time periods where reproduction was assessed for both Runs 1 and 2 was 3. The numbers of replicate colonies for Runs 1, 2, and 3 were 10, 14, and 6, respectively. Growth was measured in Run 1 for eight weeks, in Run 2 for six weeks, and in Run 3 for four weeks after settlement. Colony fecundity was assessed for 30 days in Runs 1 and 2. *P* values <0.05 are shown in bold type.

1986, Hunt and Scheibling 1997). Postsettlement mortality can be due to micropredators, strong competition, or starvation (reviewed by Hunt and Scheibling 1997). Competition and micropredation seems unlikely in this instance as larvae were settled on plates that were initially free of other organisms. *Bugula neritina* colonies are preyed upon by fish (Keough 1986), but it is hard to imagine such small differences in larval size resulting in size-specific predation (Pechenik 1999). Colonies originating from larger larvae may be more resistant to periods of low food because they have more reserves or develop larger feeding structures. Wendt (1996) found that *B. neritina* larvae that had their metamorphosis artificially delayed had smaller lophophores once they metamorphosed. Colonies originating from smaller larvae may also have smaller feeding structures, although this remains to be tested.

In Florida, mortality continued throughout the experiment and this mortality was not size dependent after two weeks. These results highlight the importance of monitoring offspring survival over as much of the life history as possible. From our results, it appears that colonies that originate from larger larvae have a selective advantage when mortality is low (i.e., at Williamstown ~39%) and occurs early in post-metamorphic life. When mortality was high and continued throughout the life of colony (i.e., Florida, total mortality = ~77%), the benefits of increased offspring size were greatly reduced. Interestingly, Moran and Emlet (2001) found similar effects of offspring size on survivorship in the field; larger *Nucella ostrina* hatchlings had greater survivorship than smaller hatchlings but this advantage was greatly reduced in more severe environmental conditions. In contrast, the benefits of increased offspring size have been shown to be greater in more severe environmental conditions in a number of species (e.g., Mousseau and Fox 1998, Einum and Fleming 1999). Clearly, the interaction between the offspring size and environmental quality is not straightforward.

The effects of larval size on colony growth persisted for at least 30 days after metamorphosis at both sites. At Williamstown, this relationship was mitigated by the onset of reproduction. In both runs where reproduction was assessed, increased larval size resulted in greater fecundity and in one run, increased offspring size also resulted in earlier reproduction. The effects of offspring size on reproduction may be a direct effect of original larval size, or may be an indirect effect, determined primarily by offspring colony size. Fecundity rises with colony size in many colonial invertebrates, reflecting increases in the number of zooids capable of reproducing, and the onset of reproduction appears to be size dependent in several populations of *Bugula neritina* (Keough 1986, 1989), so larger colonies may reproduce sooner after settlement. By reproducing sooner, these colonies may be able to produce more larvae throughout the reproductive season.

One fascinating result is that large colonies produce large larvae that give rise to large larvae in the next generation. The ultimate mechanism for this grandparent effect (cf., ''grandfather effects'' in Reznick 1981) is unclear. Larval size could be largely under genetic control and therefore maternal larval size could directly affect larval size through subsequent generations (e.g., Sinervo and Doughty 1996). Alternatively, this effect could be the result of two independent relationships, between larval size and colony growth, and colony size and larval size. An appropriate next step will be to determine how plastic larval size is when colonies of a given size are subjected to changing food levels or other stresses. Within a number of species from a wide range of taxa, it is apparent that offspring size is determined by maternal size (reviewed in Sakai and Harada 2001). In addition, offspring size affects juvenile growth and may influence adult size at reproduction (e.g., Einum and Fleming 1999, Moran and Emlet 2001). Therefore, the cross-generational grandparent effect of offspring size observed here, even if it does not have a genetic basis, may also occur in other systems

Larger colonies produce larger larvae that are much more likely to survive and reproduce at a greater rate than smaller larvae. Thus, there is strong coupling between the ecology of larval and post-larval life-history stages. In addition, the relative strength of this coupling appears to differ between localities.

Variation in larval condition or quality, caused by larval experience, can have strong effects on post-settlement performance (Pechenik et al. 1998). Our results show that, for non-feeding larvae, the initial provisioning of those larvae has equally strong effects, which can persist through the adult stage and into subsequent generations, far longer than has been shown before. These results suggest that some of the well documented variability in recruitment of marine invertebrates (e.g., Underwood and Keough 2001) may be explained by variation in larval quality. We have shown that offspring size positively affects a number of important adult life-history characteristics and may be a more important determinant of adult and second-generation phenotype than previously recognized.

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